

# SILICEOUS DINOFLAGELLATE THECAL FOSSILS FROM THE EOCENE OF BARBADOS

by IAN C. HARDING and JANE LEWIS

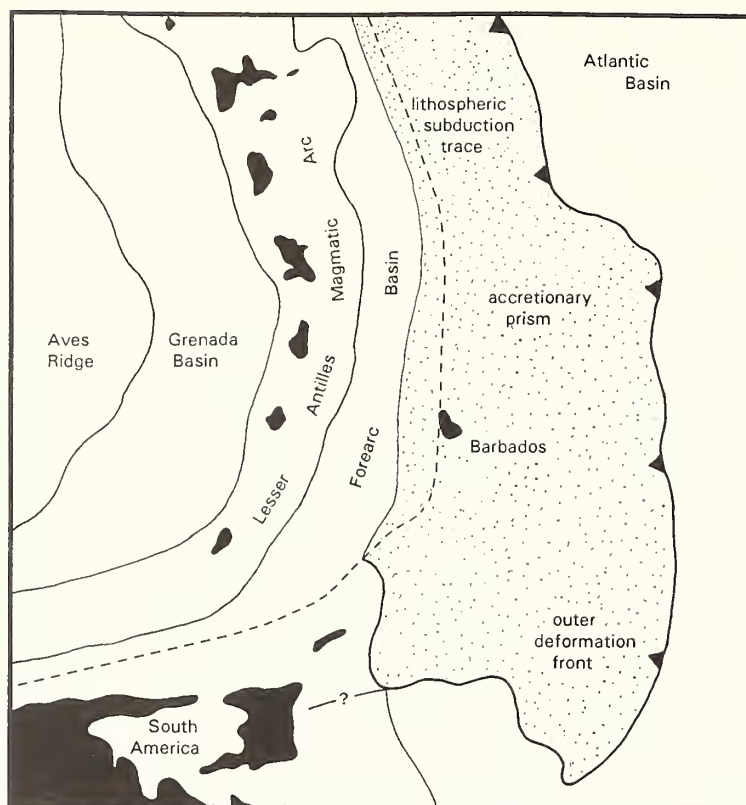
**ABSTRACT.** Detailed sampling of Palaeogene sediments from Barbados has resulted in the rediscovery of the type locality of the rare siliceous dinoflagellate *Peridinites*. Electron microscopic examination has revealed that *Peridinites* can only be interpreted as the remains of dinoflagellate motile thecate cells, rather than hypnozygotic cysts; it thus represents the first unequivocal example of a fossil dinoflagellate theca. Dinoflagellate cysts have also been found and identified as belonging to *Lithoperidinium*. Both *Peridinites* and *Lithoperidinium* are valid genera, and are interpreted as being primarily silicified. *Peridinites* is thus the only known dinoflagellate capable of secreting siliceous thecal plates.

DINOFLAGELLATES may include in their life-cycles a motile stage (often a tabulated theca of cellulosic plates) and a resting cyst stage formed after sexual reproduction. The thecate motile stages are conventionally believed not to be represented in the fossil record, because of the volatile nature of the cellulose of which they are constructed (Allison and Briggs 1991). Dinoflagellate cysts, however, are usually composed of the complex biopolymer 'sporopollenin'; more rarely, additional calcareous layers are secreted. The dinoflagellate fossil record is conventionally envisaged as being almost exclusively composed of cysts.

Lefèvre (1933a) briefly described a new dinoflagellate genus, *Peridinites* (with seven species), from a single sample of Palaeogene radiolarite from Barbados. This is the more important of only two known genera of siliceous dinoflagellate body-fossils (a few motile cells such as species of *Actiniscus* (Ehrenberg) Ehrenberg, 1843 produce siliceous internal spicules); the second is *Jusella* Vozzhennikova, 1963. Additional species referable to these genera have only been described from Russian borehole material (four species: Deflandre 1940; Vozzhennikova 1963, 1967) and New Zealand outcrop material (one species: Deflandre 1933). Finally, specimens which may be referable to *Peridinites* were illustrated by Dale (1983), from material dredged from the Norwegian Sea. All specimens were isolated from poorly dated radiolarites or diatomites, none being better defined than of a 'Palaeogene' age.

Marine *Peridinites* displays the earliest known example of cinctioid tabulation, an organization characterized by an inverted pentagonal second anterior intercalary plate (Bujak and Davies 1983). Furthermore, it is not known whether *Peridinites* represents siliceous thecae, primarily siliceous cysts, or secondarily silicified cysts. It has been suggested (e.g. Bujak and Davies 1983, p. 34) that *Peridinites* was indeed primarily silicified, but no definite statement as to the cyst or thecal affinity of the fossil has been proposed.

The aim of this study was to employ high-resolution microscopic techniques to elucidate the detailed morphology of the fossils, and to identify the stage in the dinoflagellate life-cycle that they represent. The permanently mounted nature of the type material, held in the Deflandre Collection of the Museum d'Histoire naturel Paris, and the small size of the specimens (25–50  $\mu\text{m}$  in diameter) necessitated the collection of new topotype material from Barbados.



TEXT-FIG. 1. Geological setting of Barbados, showing the position of the outer deformation front of the accretionary prism and the inferred position of the subduction trace of the Atlantic plate (after Speed, 1983).

## TYPE LOCALITY AND BARBADIAN GEOLOGY

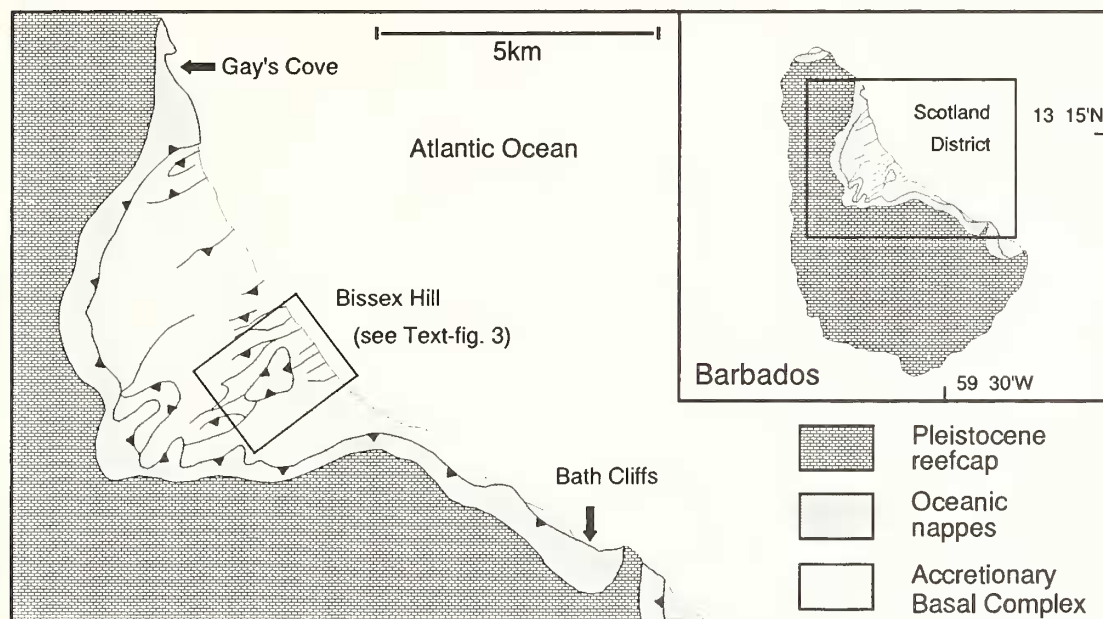
### *Type locality*

The material examined by Lefèvre (1933*a*) in his original description of *Peridinites* was taken from collections of Barbadian material already held in the Laboratoire de Cryptogamie of the Museum d'Histoire naturel, Paris. The sample used for the original descriptions came from the collection of Petit, the vial of prepared material bearing the brief label 'Diatomées fossiles. Springfield, Barbades'. Subsequently, Lefèvre (1933*b*) discovered additional specimens in another set of samples previously prepared by Rataboul and Bourgoigne. The greatest number of specimens was isolated from a tube labelled simply 'Barbades moyen'. No additional information is given in any of Lefèvre's papers regarding sample provenance. The present curator of the collections in the Laboratoire de Cryptogamie, Dr M.-T. Venec-Peyre, was unable to provide any further data which would aid in identifying the type locality or the date of sample collection. Examination of the type slides (by ICH) indicated that the type lithology was biogenic sediment rich in radiolaria, diatoms and sponge spicules.

Springfield (as on Lefèvre's label) is one of many sugar cane plantations on Barbados. Although the boundaries of these estates have been modified in recent decades, the name implies that the samples were probably collected in the vicinity.

### Barbadian geology

During the period in which the samples were collected, Barbados was believed to have layer-cake stratigraphy (Jukes-Browne and Harrison 1892). More recently, the geology of the north-eastern quadrant of the island (known as the Scotland District) has been revised in the light of plate tectonic theory (Speed and Larue 1982; Speed 1985). Barbados is now known to be an emergent part of the Barbados accretionary prism, which lies above the descending North American plate, and eastwards of the Caribbean plate (Text-fig. 1). Springfield is located near to Bissex Hill, in the Scotland District (Text-fig. 2).

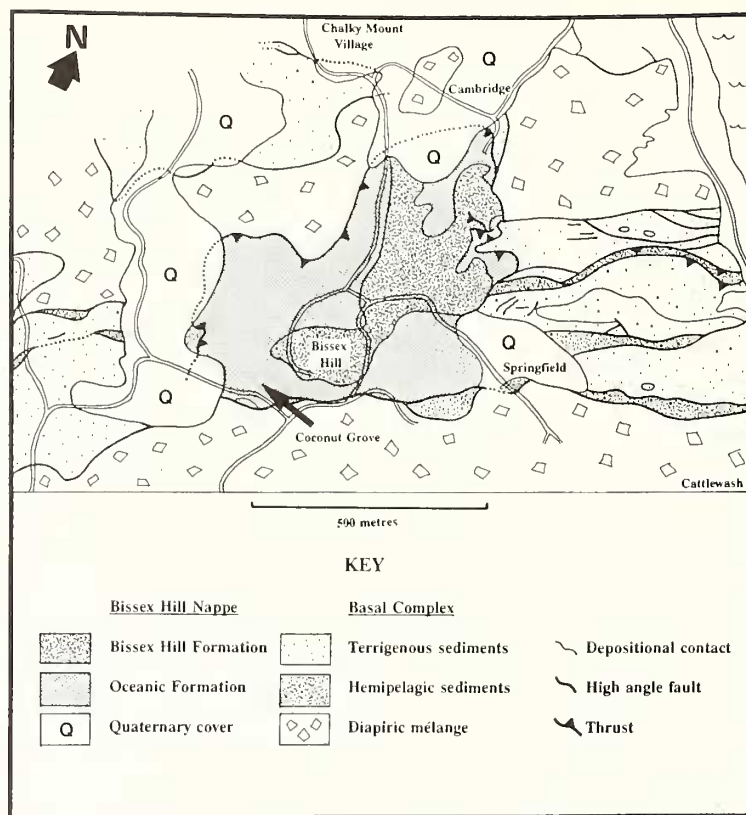


TEXT-FIG. 2. Inset shows island of Barbados, indicating northeastern Scotland District. Main map shows the geological units of this district and the location of Bissex Hill (after Speed, 1985).

The geological structure of the area around Springfield is complex, and consists of three main structural units (Larue and Speed 1984; Text-fig. 3). The first of these units consists of a series of east-northeast striking fault-bounded packets of sediments which form part of the basal accretionary complex of the island. Individual fault packets are composed of one of two lithological associations: a terrigenous suite (formerly known as the Scotland Series), and a hemipelagic suite (dominantly radiolarites, radiolarian mudstones and thin sandstones). Immediately to the west of Springfield lies the second structural unit, a subhorizontal thrust-sheet, the Bissex Hill Nappe, composed of calcareous biogenic sediments – the Oceanic Beds and the Bissex Hill Formation. These sediments have been backthrust over the Basal Complex from the Lesser Antilles fore-arc basin to the west (Text-fig. 1). The third structural unit is a diapiric mélangé, formerly known as the Joes River Formation. The mélangé is composed of mudstone, quartzose turbidite, radiolarite and calcareous pelagite clasts in a mudstone matrix.

### Sample provenance

All the lithologies discussed above occur within 500 m of Springfield plantation house and, except for the terrigenous suite of the Basal Complex, could have yielded the specimens of *Peridinites*. A representative collection of samples from all lithologies cropping out in the vicinity of Springfield



TEXT-FIG. 3. Local geology around Springfield plantation house, northeastern Barbados, showing structural complexity of Basal Complex thrust slices overlain by Oceanic Nappe and intruded by diapiric mélange (after Larue and Speed, 1984).

was taken for examination. Samples were obtained from the hemipelagites of Packets 15 and 17 (of Larue and Speed 1984) in the Basal Complex, from the Oceanic Beds at Coconut Grove, from the Bissex Hill Formation on the summit of Bissex Hill, and also from clasts in the mélange (Packet 18). The specimens described here were isolated from the samples collected at Coconut Grove in the Oceanic Formation. These samples were buff-coloured, radiolarian-diatom pelagic oozes.

Radiolarian analysis (by ICH and Paul Robinson, Southampton) has dated the samples as being of mid Eocene age, belonging to the *Thyrsocyrtis triacantha* Zone (Sanfilippo *et al.* 1985; Pl. 1, fig. 8), on the occurrence of the eponymous species and *Theocotyle venezuelensis* Riedel and Sanfilippo, 1970. The siliceous component of the samples, although dominated by radiolaria, is also rich in centric diatoms and sponge spicules, with a similar species composition to the original type material.

#### MATERIALS AND METHODS

Various techniques were explored to determine the optimum methods for extracting the *Peridinites* fossils from the radiolarites, and a standard method used in the preparation of radiolaria produced the best results. Samples were broken into small pieces and soaked in Calgon (sodium hexametaphosphate) to break up the clay minerals; they were then decalcified using fifty per cent hydrochloric acid, followed by a treatment with ten per cent hydrogen peroxide to oxidize any



obscuring organic matter. Samples more resistant to these treatments responded to gentle heating of the processing reagents. The rare specimens of *Peridinites* were concentrated by sieving into separate size fractions of  $> 125 \mu\text{m}$ ,  $125\text{--}63 \mu\text{m}$ ,  $63\text{--}40 \mu\text{m}$ , and  $40\text{--}20 \mu\text{m}$ .

*Peridinites* proved to be most common in the  $40\text{--}20 \mu\text{m}$  fraction, although they were still extremely rare, occurring at a frequency of approximately one siliceous dinoflagellate per 100 000 radiolaria. The different size fractions were examined in distilled water using an Olympus BH-2 transmitted light microscope. Specimens were isolated by micropipette, and mounted on squares of film which were attached to aluminium electron microscopy stubs. Selected specimens were coated in carbon to allow X-ray compositional microanalysis to be conducted, in a JEOL JSM-6400 scanning electron microscope fitted with a Tracor Series II energy dispersive X-ray analysis system. Following analysis, specimens were sputter-coated with gold for photomicrography.

The specimens illustrated in this paper are housed in the Sedgwick Museum, Department of Earth Sciences, University of Cambridge, UK, under the catalogue numbers SM X.24547–X.24553.

## RESULTS

### *Dinocysts versus dinoflagellate thecae*

The features which can be used to discern a dinoflagellate cyst from a motile theca have been discussed by Dale (1983) and Evitt (1985) and are listed in Table 1. The specimens identified as belonging to *Peridinites*, fulfilled all of the morphological criteria required for the interpretation of *Peridinites* as fossils of the motile thecate stage in the dinoflagellate life-cycle.

TABLE 1. Comparison of morphological features found on motile dinoflagellate thecae and non-motile dinoflagellate cysts.

Peridiniacean motile cell features	Peridiniacean cyst features
Articulated plates	Continuous wall layer
Functional sutures	Non-functional parasutures
Plate overlap	Reflected overlap
Functional, depressed cingulum and sulcus	Often discontinuous ridges or grooves, ornamented areas, or not expressed
Functional flagellar pore	Flagellar scar
Trichocyst pores	Reflected pores, often represented as spines
Apical pore	Apical plate (P plate)
Ecdysal opening	Archaeopyle

1. The fragmentary nature of the *Peridinites* specimens is not due to mechanical breakage of the fossils (this can be seen around the cingulum of the specimen in Plate 1, figure 2) but rather to the dissociation of the individual siliceous plates of which the specimens are composed (see Pl. 1, fig. 4, Pl. 2, fig. 3). The fragmentation of the specimens followed lines of weakness along the boundaries between the individual plates and are not intraplate fractures. This implies that the junctions between the plates are functional sutures, rather than the thecamorphic non-functional parasutures found on some dinocysts (Gocht 1983), i.e. they are merely reflections of thecal features on the surface of the cyst. This is the most powerful argument for the interpretation of *Peridinites* as a motile thecate organism.

2. The plate overlap direction (Text-fig. 3A) is just as it would appear on the external surface of a modern theca. This contrasts with many sub-thecal fossil cysts, in which the paraplate overlap direction is inversely related to the plate overlap on the parent theca (Harding 1988).

3. The cingulum and the sulcus appear eminently capable of housing functional flagella, as

there are no obstructions along either, which would have inhibited normal flagellar function (e.g. Pl. 1, fig. 6).

4. Three types of pores are identified on *Peridinites*, which penetrate the siliceous wall from the external surface to the interior of the fossil (Pl. 1, figs 1, 5, 11). Whilst some dinocysts possess wall perforations (claustra) these never penetrate the hermetically sealed inner wall layer; such perforations are common in dinoflagellate thecal plates. In addition, a large pore is found within the apical horn (Pl. 1, fig. 12), of identical morphology to those found on modern peridinoid thecae (Dodge and Hermes 1981; Toriumi and Dodge 1993). A second pore-type is found at the convergence of cingulum and sulcus (Pl. 1, fig. 5) and presumably served for the emergence of a pair of flagella. The most common pores are interpreted as trichocyst openings, as their distribution in intraplate areas and lining the cingulum (Pl. 1, fig. 6) echoes their placement on modern peridinoids (Dodge 1983; Lewis 1990).

5. The sculpture of these fossils is particularly reminiscent of that of modern gonyaulacoids (Dodge 1989), although no systematic relationships are inferred by this.

6. Intercalary growth bands have not been observed on any of our specimens, although in the generic description of *Peridinites*, Lefèvre (1993a) described the occasional occurrence of transverse striations across the sutures. This is consistent with the interpretation of *Peridinites* as representing the motile stages of the life cycle, and including both vegetative thecae and zygotic thecae, as the latter display more prominent volume growth and thus wide intercalary growth bands.

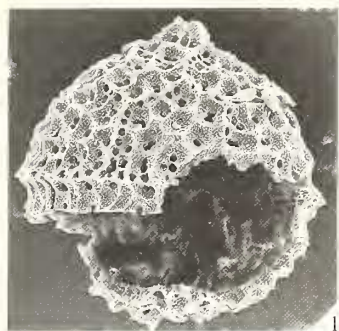
7. *Peridinites* displays a post-cingular opening formed by the loss of the three plates 2'', 3'' and 4'' (Pl. 1, fig. 4). If these specimens were vegetative thecae, their cell contents must have been able to escape from the cell during gametogenesis, a process known as ecdysis. Thus, rather than being excystment openings or archaeopyles, these features would be ecdysal openings. Although antapical archaeopyles have been suggested for three dinoflagellate genera (Wall and Dale 1971; McClean 1973), *Peridinites* is the only morphotype yet identified with an opening developed in the post-cingular plate series. An analysis of the plate overlap patterns of the epitheca revealed the second anterior intercalary to be the epithecal keystone plate, as is the case with modern protoperidinoids. Assuming that these siliceous thecae produced cysts, this observation suggests that the 2a paraplate may have been involved in archaeopyle formation. The specimens of *Lithoperidinium oamaruense* Deflandre, 1933, and *L. rossicum* Deflandre, 1940 examined by ICH in Paris, and here believed to be of cyst affinity, do not contradict this statement.

#### EXPLANATION OF PLATE 1

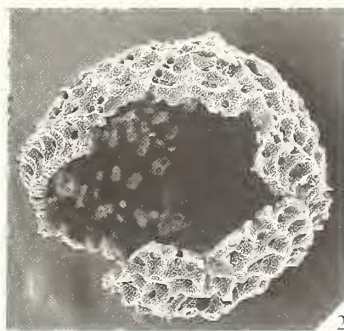
Figs 1–7, 9–12. *Peridinites piriformis* Lefèvre; sample COC4; Coconut Grove, near Springfield, Barbados; Oceanic Formation, Eocene. 1–5, SM X.24547. 1, oblique dorsal view showing hypothecal ecdysal opening; note damaged 4'' and 5'' plates, and extensive development of trichocystal perforations in thecal plates;  $\times 3000$ . 2, oblique right lateral view, showing damage to cingular and precingular 4'' and 5'' plates;  $\times 3000$ . 3, antapico-dorsal view clearly showing the ecdysal opening resulting from the loss of plates 2''–4'';  $\times 3000$ . 4, antapical view illustrating the large hypothecal opening and the two small antapical plates;  $\times 3000$ . 5, internal view showing large opening, interpreted as the flagellar pore, and smaller perforations, interpreted as trichocyst pores; note that pores penetrate the wall;  $\times 7500$ . 6, SM X.24548; ventral view of isolated epitheca, note asymmetrical nature of plate 1', cingulum displaced by one cingulum width, and apical prominence;  $\times 3400$ . 7, SM X.24549; internal view of isolated epitheca showing large apical pore with plate 3' immediately above; note that the grooves parallel to the plate margins are only found on overlapping plate margins;  $\times 6000$ . 9, SM X.24548; detail of plate 1'', showing single rows of trichocyst pores along overlapped margins of plate 2' at top of picture and plate 2'' to right of picture;  $\times 6000$ . 10–12, SM X.24550. 10, apico-left lateral view, showing first precingular plate to left;  $\times 3300$ . 11, apical view; note concentrations of trichocyst pores; first precingular plate to bottom;  $\times 3000$ . 12, apical view of large, raised, open apical pore surrounded by trichocyst pore openings; note surface texture of fused silica granules; etched appearance may be due to incipient silica dissolution;  $\times 15000$ .

Fig. 8. *Lithocytrix vespertilio* Ehrenburg; sample COC4; Coconut Grove, near Springfield, Barbados; Oceanic Formation, Eocene; X.24560;  $\times 370$ .

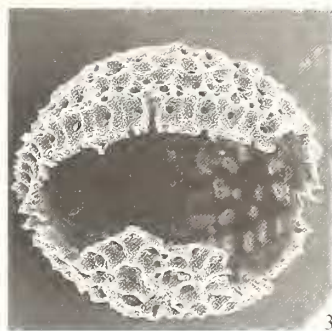




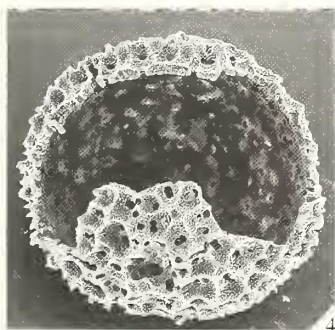
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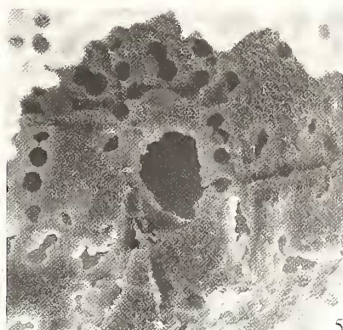
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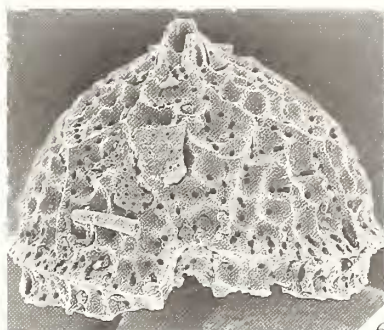
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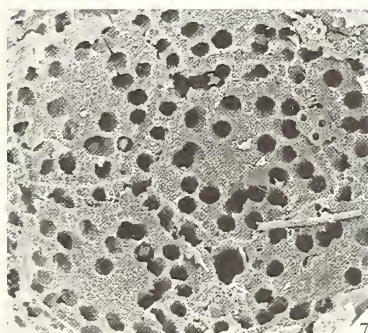
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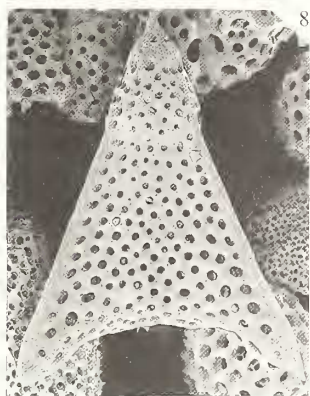
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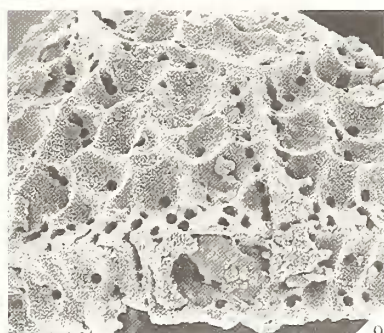
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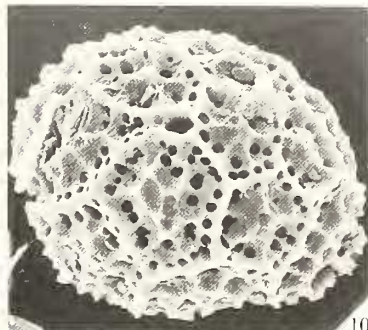
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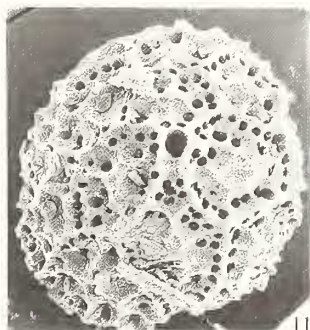
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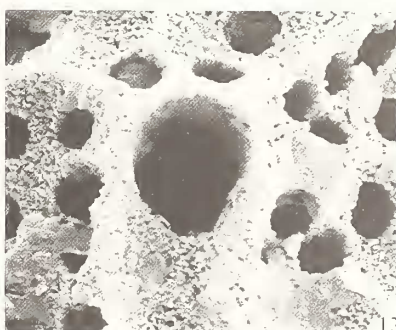
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11



12

In the authors' opinion, all of the features displayed by *Peridinites* are consistent with its interpretation as a motile thecate organism; indeed no morphological features have been discovered which would argue against this conclusion. After extensive discussion, Deflandre (1933) also concluded that this was likely. Thus, we interpret specimens of *Peridinites* as siliceous organisms, with morphological characteristics indicating they were motile thecate dinoflagellates. *Peridinites* is the only genus of unequivocal fossil dinoflagellate thecae yet identified.

### *Primary versus secondary silicification*

X-ray microanalysis of *Peridinites* indicated an entirely siliceous composition. One modern dinoflagellate, *Thoracosphaera* Kamptner, 1927, produces mineralized vegetative cells (Tangen *et al.* 1982), but these are calcitic and not siliceous. Only the modern *Ceratium hirundinella* (O. F. Muller) Bergh, 1882 and *C. furcoides* (Levander) Langhans, 1925 secrete small siliceous granules on the external surface of their organic walled cysts (Chapman *et al.* 1982). All other dinoflagellates known to secrete silica do so in the form of internal sclerites (e.g. the star-shaped pentasters of actiniscids).

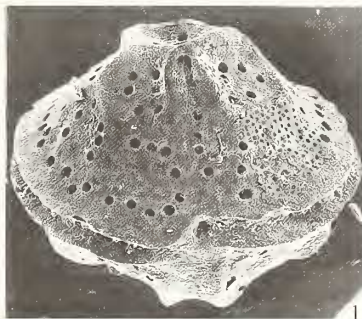
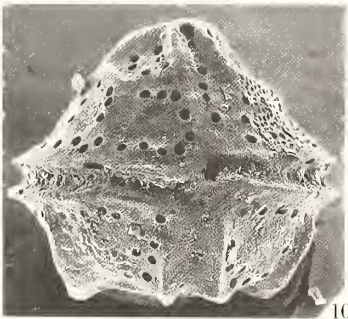
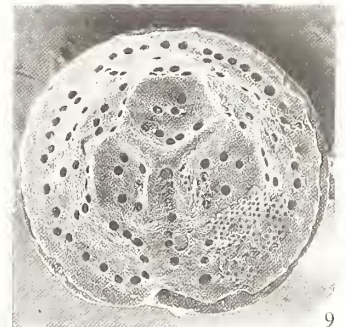
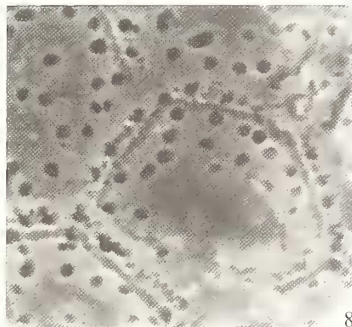
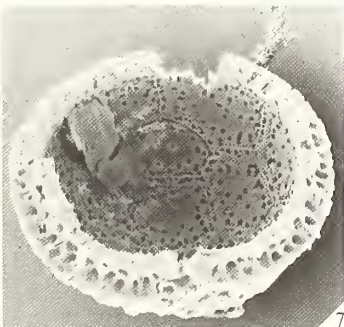
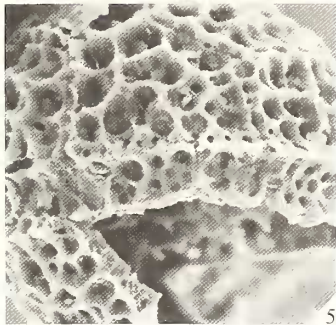
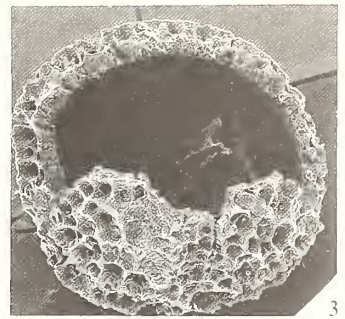
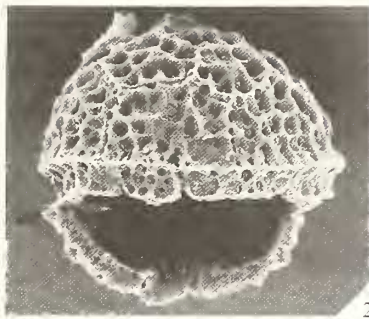
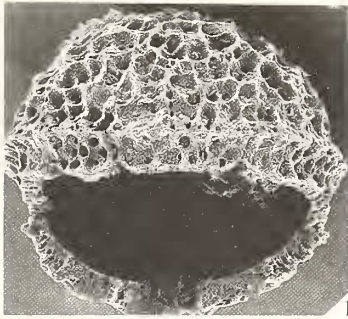
How then can the composition of *Peridinites* be explained? When described by Lefèvre (1933a, 1933b) *Peridinites* was believed to have been a secondarily silicified body fossil, a view also expressed by Balech (quoted in Bujak and Davies 1983, p. 34). However, Deflandre (1933) pointed out that they may have been primarily siliceous cells, a view supported by Bujak and Davies (1983, p. 34). Although difficult to prove, secondary silicification would need to be extremely rapid, prior to bacterial breakdown of the cellulosic plates. The samples all show indication of intensive bioturbation in well aerated bottom waters at the site of deposition, making such bacterial activity a strong likelihood. Indeed, it is unusual to encounter cellulosic dinoflagellate thecae in modern marine sediments (JL, personal observation). Furthermore, there is no evidence for the silicification of other volatile compounds in the residues, and the samples show no evidence of silicification of the well preserved calcareous microfossils, which co-occur in the topotype material. Examination of the siliceous component of the residues indicates active silica dissolution, especially of the more fragile centric diatoms, rather than secondary silicification. Thus, we interpret specimens of

### EXPLANATION OF PLATE 2

Figs 1–8. *Peridinites sphaericus* Lefèvre; sample COC4; Coconut Grove, near Springfield, Barbados; Oceanic Formation, Eocene. 1–5, SM X.24551. 1, dorsal view showing large hypothecal ecdysal opening and clearly functional sutures, especially between cingular plates;  $\times 2700$ . 2, oblique left dorsal view showing low apical prominence and cinctoid 2a plate with raised margins indicating overlap of all adjacent plates;  $\times 2500$ . 3, antapical view showing ecdysal opening formed by loss of plates 2'', 3'' and 4''; antapical and posterior sulcal plates have also been lost; note that all plates have separated along functional sutures;  $\times 2500$ . 4, oblique left lateral view showing functional sutures between individual plates, large plate above the cingulum is 3';  $\times 3700$ . 5, detail of entire plate margins, indicating fragmentation of theca is due to separation of plates along functional sutures; plate margin at bottom of micrograph is the 1''/2'' suture, to the left is the cingulum/2'' suture;  $\times 8000$ . 6, SM X.24552, detail of apical tabulation showing prominent apical pore, with 3' to the right of this and cinctoid 2a plate to mid-right;  $\times 5000$ . 7–8, specimen lost. 7, internal view of isolated epitheca, showing reflected tabulation; note apical pore to right centre and first apical plate extending from this at 45°;  $\times 2700$ . 8, detail showing apical pore and plate 3'; note overlapping plates have a groove parallel to the plate margin, the suture between overlapping and overlapped plate margins is ragged and bisects trichocyst pores;  $\times 7000$ .

Figs 9–12. *Lithoperidinium* sp. sample COC4; Coconut Grove, near Springfield, Barbados; Oceanic Formation, Eocene; SM X.24553. 9, apical view showing prominent parasutural ridges bounding plates 2'–4';  $\times 1600$ . 10, ventral view showing prominent flagellar pore and narrow, parallel-sided nature of the parasulcus;  $\times 1700$ . 11, apico-ventral view showing very narrow first apical paraplate leading to apical pore; microperforated region on paraplate 1'' is an adherent diatom fragment;  $\times 1700$ . 12, oblique, apical-right lateral view; note long, narrow 6'' and narrow, asymmetrical 5'';  $\times 1700$ .





*Peridinites* as being siliceous organisms, this primary mineralization leading to the fossilization of the motile thecate stage.

# SYSTEMATIC PALAEOLOGY

*Discussion.* Re-examination of the type material of *Peridinites* Lefèvre, 1933a and *Lithoperidinium* Deflandre, 1933 (by ICH), has indicated the dissimilarity between the two genera. Whereas *Peridinites* is thin-walled, and commonly incomplete and fragmentary in its preservation, specimens of *Lithoperidinium* are much more robust, possess a wall at least three times the thickness of that of *Peridinites*, and yet are of approximately the same dimensions. Optically, the sutural features of *Lithoperidinium* appear non-functional. For these reasons, we do not follow the synonymy of Deflandre (1945) and Norris and Sarjeant (1965), who designated *Lithoperidinium* Deflandre, 1933 as a synonym of *Peridinites* Lefèvre, 1933a. Neither do we accept the use of *Lithoperidinium* as the senior synonym (Fensome *et al.* 1993; Lentin and Williams 1993) but retain both genera. *Peridinites* is a siliceous dinoflagellate fossil, here identified as the thecal stage in the life cycle, rather than a hypnozygotic cyst; we herein emend this genus. *Lithoperidinium* is interpreted as being the fossilized cyst stage of the life cycle and is also emended. We follow the classification scheme of Fensome *et al.* (1993), but note that their description of Lithoperidinioideae mentions only the cyst stage of the life cycle. We expand this to incorporate the thecate stage of the life cycle and hence include *Peridinites* in this subfamily. The discrimination of *Jusella* Vozzhennikova, 1963 from *Lithoperidinium* Deflandre, 1933 is regarded as being based on morphological features not of generic rank, making *Jusella* a later synonym of *Lithoperidinium*.

Division DINOFLAGELLATA (Bütschli, 1885) Fensome *et al.*, 1993

Subdivision DINOKARYOTA Fensome *et al.*, 1993

Class DINOPHYCEAE Pascher, 1914

Order PERIDINIALES Haeckel, 1894

Family PERIDINIACEAE Ehrenberg, 1832

Subfamily LITHOPERIDINIOIDEAE (Deflandre, 1945) Fensome *et al.*, 1993

Genus PERIDINITES Lefèvre, 1933a emend. nov.

Type species. *Peridinites parvulus* Lefèvre, 1933a.

*Emended diagnosis.* Subspherical to pyriform dinoflagellate thecal fossils. Epitheca and hypotheca of approximately equal dimensions, separated by a prominently indented, descending cingulum. Sulcus confined to hypotheca in the form of a parallel-sided longitudinal furrow. Theca composed of heavily sculptured plates completely perforated by many trichocyst pores and separated one from another by functional sutures. Tabulation: **Po**, **4'**, **3a**, **7''**, **?6c**, **5'''**, **2'''**, **?s**. Hypothecal ecdysal opening comprising at least **2'''–4'''**.

*Peridinites piriformis* Lefèvre, 1933a

Plate 1, figures 1–7, 9–12; Text-figure 4

v\*1933a *Peridinites piriformis* Lefèvre, p. 417.

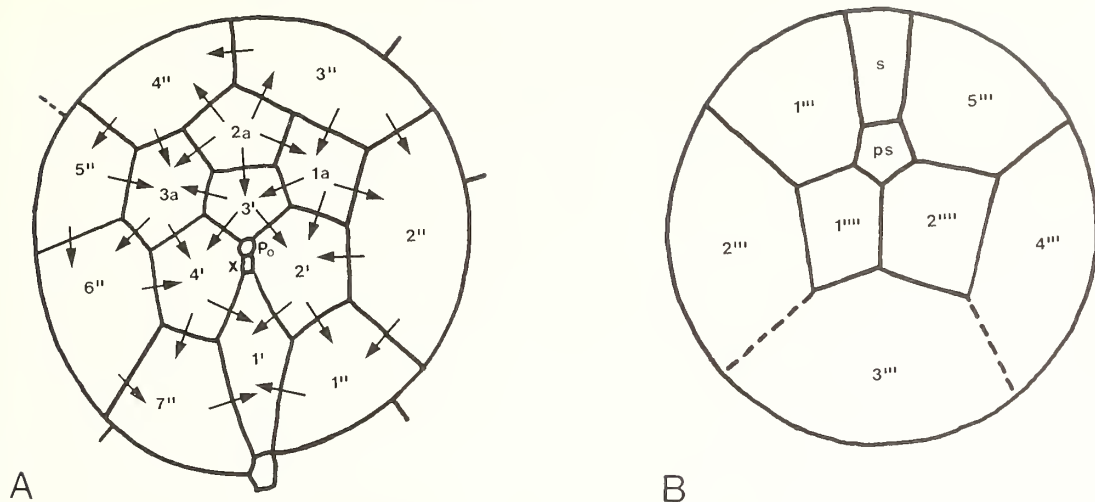
v\*1933b *Peridinites piriformis* Lefèvre; Lefèvre, p. 225, figs 17–18.

## Emended description

*Shape.* Pyriform, with a short, pronounced apical horn (Pl. 1, figs 1, 6). There is no indication of primary dorso-ventral compression. Epitheca slightly larger than hypotheca.

*Wall structure.* The single wall is up to 2  $\mu\text{m}$  in thickness. The sculpture takes the form of an irregular reticulum consisting of laevigate muri rising to a sharp, knife-edge culmination. The lumina (1–3  $\mu\text{m}$  in diameter) are fairly deeply excavated and may contain one or more pores at the base. These trichocyst pores (0.5  $\mu\text{m}$  in diameter) fully penetrate the thecal wall (Pl. 1, figs. 5, 7). The majority of trichocyst pores are regularly lined





TEXT-FIG. 4. A, epithecal tabulation and plate overlap patterns (as far as have been discerned) of *Peridinites piriformis*. Tabulation and plate overlap, as far as can be discerned is the same for *P. sphaericus*. B, hypothecal tabulation of *P. piriformis*. Tabulation, as far as can be discerned, is the same for *P. sphaericus*.

up along the plate sutures, although a few are irregularly scattered in intratabular positions (Pl. 1, fig. 7). The ovate apical pore ( $1.5 \times 2.0 \mu\text{m}$ ) is surrounded by a raised collar and is of the typical peridinioid form (Pl. 1, fig. 12).

**Cingulum.** Indented and slightly offset by about one cingular width. Three cingular sutures have been found adjacent to 1'', 2'', 3''. It has not been possible to analyse the right-hand side of the specimens. Referring to the discussion under *P. sphaericus*, it seems likely that this species has a full complement of six cingular plates.

**Sulcus.** Parallel-sided, slightly depressed but tabulation poorly defined. A single ovate flagellar pore ( $3 \mu\text{m}$  in diameter) is located where the cingulum joins with the sulcus.

**Tabulation.** Externally, the overlapping margins are bounded by sharp-edged ridges, the overlapped margin showing a linear concentration of trichocyst pores. Internally, the overlapping plates bear a linear groove parallel to the plate margin, the suture between plates being a fissure close to the line of trichocyst pores. The keystone plates are 2a and 3''. The epithecal tabulation is characteristically cinctioid – Po, x, 4', 3a, 7'' (Pl. 1, fig. 1; Text-fig. 4A). The apical pore plate (Po) is circular and is joined to the wide first apical plate by a short canal plate (x) (Pl. 1, figs 6–7). The first and second intercalaries are pentagonal with a hexagonal third intercalary plate. Ventral epithecal tabulation is ortho. Hypothecal tabulation (5''', 2''') is known in more detail than that of *P. sphaericus*, as one specimen has been observed with antapical plates in place (Pl. 1, fig. 4; Text-fig. 4B). Antapical plates are relatively small in comparison to the post-ingular series. The ecdysal opening is formed by the loss of 2'''–4'''.

**Dimensions.** Equatorial diameter (26) 27 (28)  $\mu\text{m}$  (6 specimens measured).

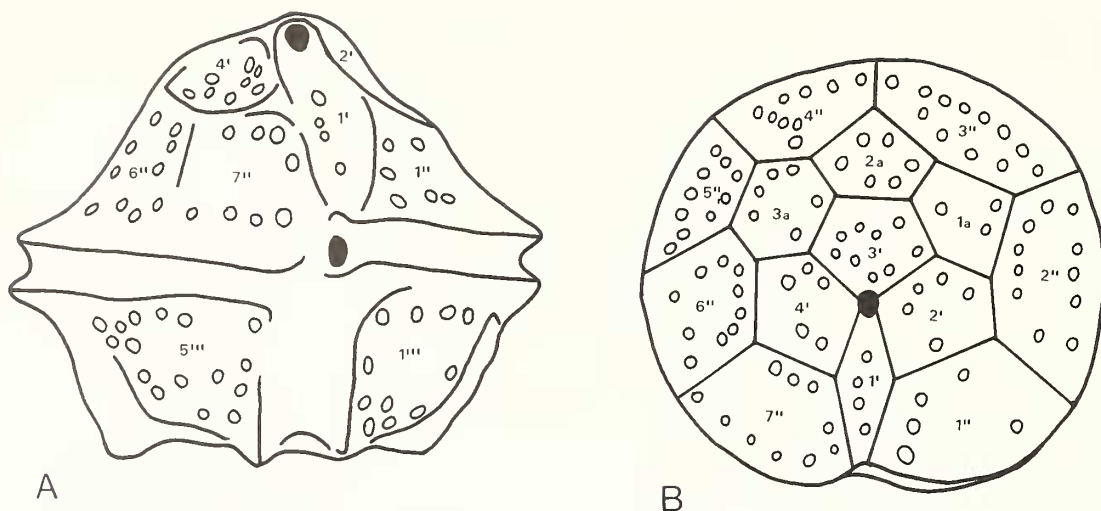
**Remarks.** Examination of the type specimens in Paris, and the collection and study of new topotype material from Barbados, has allowed a precise redescription of the species. The specimens here assigned to *P. piriformis* are directly comparable to the size range given by Lefèvre (1933b). The thecal nature of the specimens is emphasized.

*Peridinites sphaericus* Lefèvre, 1933a

Plate 2, figures 1–8

v\*1933a *Peridinites sphaericus* Lefèvre, pp. 416–417.





TEXT-FIG. 5. A, ventral tabulation of *Lithoperidinium* sp. B, epicystal tabulation of *Lithoperidinium* sp.

v\*1933b *Peridinites sphaericus* Lefèvre, pp. 223–224, figs 13–14.

v\*1933b *Peridinites sphaericus* var. *minor* Lefèvre, p. 224, text-fig. 24.

1973 *Peridinites sphaericus* ssp. *minor* Lentin and Williams, p. 111.

### Emended description

*Shape.* Ambitus subspherical (Pl. 2, fig. 2). No evidence of primary dorso-ventral compression. Epitheca slightly larger than hypotheca, and produced into a very short, blunt apical horn.

*Wall structure.* The single wall layer is up to  $2\ \mu\text{m}$  thick (Pl. 2, fig. 4). The wall is fragile and prone to fragmentation along the plate sutures. Sculpture consists of an irregular raised reticulum consisting of mural ridges reminiscent of modern gonyaulacoid sculptural features. Luminal diameters range from  $0.75\ \mu\text{m}$  to  $4\ \mu\text{m}$ , with an average around  $1.5\ \mu\text{m}$  diameter. Muri width ranges from  $0.30$ – $0.75\ \mu\text{m}$ . Each lumina shows a pronounced concavity, and the majority possess a basal pore-like perforation, which fully penetrates the wall layer. These perforations, interpreted as trichocyst pores, are distributed fairly evenly over the plates, although linear concentrations are found along the adcingular sutures (Pl. 2, figs 5, 8) in a similar manner to those of modern thecae. At the apex of the horn is a circular apical pore surrounded by a low collar which is of the typical peridinioid form (Pl. 2, fig. 6).

*Cingulum.* This takes the form of a pronounced subequatorial indentation which is very slightly offset by about one half of a cingular width. Four cingular sutures have been found adjacent to plates 1'', 2'', 3'' and 7''. However, we have not been able to check to our satisfaction the areas lying adjacent to 4''–6''. Lefèvre (1933a, 1933b) does not figure or list the numbers of cingular plates, but in one diagram of *Peridinites barbadensis* a cingular suture adjacent to the 5'' plate is shown. This implies a probable complement of six cingular plates.

*Sulcus.* Parallel-sided and poorly defined.

*Tabulation.* Sutures appear fully functional, being visible on both internal and external surfaces (Pl. 2, figs 1–8). Externally, plate overlap direction is indicated by a high scalloped plate margin on the overlapping plate, the underlapped margin being of much lower relief (Pl. 2, fig. 6). Internally, the overlapping plates bear a linear groove parallel to the plate margin, the suture between plates being a fissure close to the line of trichocyst pores. The second anterior intercalary is the epithecal keystone plate overlapping all of its neighbours (Pl. 2, figs 2, 6). Epithecal tabulation is characteristically cinctioid—Po, x, 4', 3a, 7''. The apical pore plate (Po) is circular and is joined to the narrow first apical plate by a short canal plate (x). The first and second intercalaries are pentagonal with a hexagonal third intercalary plate. Ventral epithecal tabulation is ortho. The hypothecal tabulation is 5''', 2'''.

*Ecdysal opening.* The formation of an ecdysal opening appears to involve plates 2''–4'', although in most instances 1''' and 2''' are also lost (Pl. 2, fig. 3). This pattern is lost on some specimens as the removal of these plates leaves the remaining hypothecal plates unsupported leading to complete hypothecal fragmentation in many specimens (Pl. 2, fig. 7).

*Dimensions.* Equatorial diameter (29) 31.2 (35)  $\mu\text{m}$  (6 specimens measured).

*Remarks.* Examination of the type specimens in Paris, and the collection and study of new topotype material from Barbados has allowed a precise redescription of the species. Lefèvre (1933b) originally distinguished specimens of *P. sphaericus* and *P. sphaericus minor* purely on the basis of size, the former varying from 32–40  $\mu\text{m}$ , the latter from 25–30  $\mu\text{m}$ . Such size variation is commonly found amongst thecal dinoflagellates and is not deemed to be worthy of subspecific importance. The thecal nature of the specimens is emphasized.

#### Genus LITHOPERIDINIUM Deflandre, 1933

1963 *Jusella* Vozzhennikova, p. 183

*Type species.* *Lithoperidinium oamaruense* Deflandre, 1933.

*Remarks.* *Lithoperidinium* is reinstated as a genus of siliceous dinoflagellate hypnozygotic cysts. Vozzhennikova (1967) retained both *Peridinites* and *Lithoperidinium*, and furthermore introduced the new siliceous genus, *Jusella*. Following Vozzhennikova (1967) and Deflandre (1940), and using the evidence presented above, we retain both *Peridinites* and *Lithoperidinium* as separate genera; the former as a genus of thecal fossils, and the latter as a genus of cyst fossils.

The taxonomic position of *Jusella* Vozzhennikova, 1963 is less clear. *Jusella* was differentiated from the other two genera by Vozzhennikova (1967) by having larger pores, coarser sculpture and a different tabulation to the hypotheca (*sic*), showing an intermediate plate between the longitudinal furrow and the antapical plates. We do not believe that either pore size or expression of sculptural features are valid criteria on which to separate these genera. Wide variations in sculpture are to be found in single species of extant dinoflagellates (Dodge 1989; Lewis and Burton 1988). The presence of an 'intermediate plate', which would now be known as a posterior sulcal plate, is also a dubious taxonomic criterion, given the variability in the expression of tabulation reported for some dinocyst genera. Present evidence indicates that *Jusella* should be more properly viewed as a synonym of *Lithoperidinium*.

Dale (1983, fig. 26) illustrated a siliceous dinoflagellate specimen from the Eocene of the Norwegian Sea, which he identified as *Peridinites globosus*. By comparison with specimens isolated in the present study, the specimen illustrated by Dale would be more properly allocated to *Lithoperidinium*.

#### *Lithoperidinium* sp.

Plate 2, figures 9–12; Text-figure 5

#### *Description*

*Shape.* A squat, prolate spheroidal cyst with a low conical epicyst and flattened hypocyst. Dorso-ventral ambitus angular, with rectangular hypocyst outline. Equatorial ambitus subspherical, indicating absence of primary dorso-ventral compression (Pl. 2, fig. 9). Epicyst slightly longer than hypocyst, and produced into a low, blunt apical horn (Pl. 2, fig. 10).

*Wall structure.* Laevigate wall up to 5  $\mu\text{m}$  in thickness (punctate area on Pl. 2, fig. 11 is an adpressed diatom fragment). Large pores (up to 2  $\mu\text{m}$  in diameter) are the most evident feature on the external surface of the cyst being distributed in a penitabular manner. Paratabulation is indicated by low ridges on the majority of the precingular paraplates, but on the remaining apical and hypocystal paraplate series, the ridges are more pronounced and may reach 4  $\mu\text{m}$  in basal width. The position of the apical pore is marked by the meeting of the gentle ridges which surround the paraplates.

*Paracingulum*. Cyst is divided equatorially by a strongly indented paracingulum, which is offset by one paracingulum width.

*Parasulcus*. The parasulcus is little more than a shallow groove bordered by parallel ridges; detailed paratabulation is not expressed.

*Paratabulation*. As far as has been determined the paratabulation is cinctoid (Text-fig. 5). Parasutures on the precingular paraplates are not clearly defined and are marked by low ridges and penitabular pores. The remaining parasutures are better defined by low, broad ridges. Ventral epicystal paratabulation is ortho-style. The first apical plate is narrow.

*Dimensions*. 49  $\mu\text{m}$  diameter (single specimen measured).

*Remarks*. This morphotype is clearly of a different structural nature from that of the specimens here assigned to the genus *Peridinites*. The most important morphological feature which points to this form being a dinoflagellate cyst rather than a fossilized *theca* is the non-functional nature of the junctions between paraplates. The size of this specimen (and its overall morphology when observed in the light microscope), is compatible with that given by Vozzhennikova (1967) for *Jusella* (*sic*) *denticulatum*.

### CONCLUSIONS

Our initial belief was that the lack of reports of *Peridinites* was due to the biasing of sample residues by differential sieving by radiolarian workers, who routinely examine size fractions greater than 63  $\mu\text{m}$ . The greatest concentration of *Peridinites* in samples so far examined, yielded a ratio of *Peridinites* specimens to other siliceous microfossils of the order of 1:100000. This extreme rarity appears to negate any possibility of the genus being used as a routine biostratigraphical index fossil, but examination of the temporally more extensive Bath Cliffs section on Barbados (Eocene to Miocene in age) may yield data indicating greater abundance in certain time intervals.

Detailed analysis of the tabulation patterns of the species of *Peridinites* corroborate the observation by Masure (1990), that the siliceous peridinoids may have evolved from heterocapsiform ancestors in which two dorsal apical plates may have fused into a single third apical plate seen in peridinoid dinoflagellates.

A detailed light and electron microscopic elucidation of the morphology of *Peridinites*, based on type and new topotype material, indicates that the genus represents not only the first reported unequivocal dinoflagellate thecal fossils, but also the only dinoflagellates known to be capable of secreting primarily siliceous thecal plates. The discovery that *Peridinites* represents a thecal fossil has made the postulation of methods of silica secretion in the fossils difficult, due to the lack of any modern analogues amongst living thecate dinoflagellates.

*Acknowledgements*. The authors would like to express their thanks to the Natural Environment Research Council for funding this project (Grant GR9/263). We would also like to thank Bob Speed (Northwestern University, Illinois) for his expertise in the field and invaluable advice, and also to Marie-Thérèse Venec-Peyre and Jean Dejax at the Museum d'Histoire naturel, for their hospitality and assistance during ICH's examination of the type material. We are also most grateful to the following at Southampton: Daphne Woods for sample processing, Babara Cressey for assistance with electron microscopy, Barry Marsh for his photographic skills and Paul Robinson for radiolarian identifications. David Bench (University of Westminster) assisted initially with specimen analysis and translations of French publications.

### REFERENCES

- ALLISON, P. and BRIGGS, D. 1991. The taphonomy of soft-bodied animals. 120–140. In DONOVAN, S. K. (ed.). *The processes of fossilization*. Belhaven Press, London, 583 pp.
- BERGH, R. S. 1882. Der Organismus der Cilioflagellaten. Eine phylogenetische Studie. *Morphologisches Jahrbuch*, 7, 177–288.



- BUJAK, J. P. and DAVIES, E. H. 1983. Modern and fossil Peridiniineae. *American Association of Stratigraphic Palynologists, Contributions Series*, **13**, 1–203.
- BÜTSCHLI, O. 1885. Unterabteilung (Ordnung) Dinoflagellata. 865–1088. In BRONN, H. G. *Klassen und Ordnungen des Tier-Reichs, Wissenschaftlich Dargestellt in Wort und Bild*, **1**, Protozoa, Abt. 2, Mastigophora. C. F. Winter'sche Verlagshandlung, Leipzig.
- CHAPMAN, D. V., DODGE, J. D. and HEANEY, S. I. 1982. Cyst formation in the freshwater dinoflagellate *Ceratium hirundinella* (Dinophyceae). *Journal of Phycology*, **18**, 121–129.
- DALE, B. 1983. Dinoflagellate resting cysts: 'benthic plankton'. 69–136. In FRYXELL, G. A. (ed.). *Survival strategies of the algae*. Cambridge University Press, Cambridge. 144 pp.
- DEFLANDRE, G. 1933. Note préliminaire sur un péridinien fossile *Lithoperidinium oamaruense* n.g. n.sp. *Bulletin de la Société Zoologique de France*, **58**, 265–273.
- 1940. Sur un nouveau péridinien fossile, à théque originellement siliceuse. *Compte Rendu de l'Académie des Sciences, Paris*, **211**, 265–268.
- 1945. Dinoflagellés II. Flagellés incertae sedis. Fiches micropaléontologiques, series 5. *Archives originales Service Documentation, Centre National de la Recherche Scientifique*, **235**, cards 752–859.
- DODGE, J. D. 1983. Ornamentation of thecal plates in *Protoperidinium* (Dinophyceae) as seen by scanning electron microscopy. *Journal of Plankton Research*, **5**, 119–127.
- 1989. Some revisions of the Family Gonyaulacaceae (Dinophyceae) based on a scanning electron microscope study. *Botanica Marina*, **32**, 275–298.
- and HERMES, H. B. 1981. A scanning electron microscopical study of the apical pores of marine dinoflagellates (Dinophyceae). *Phycologia*, **20**, 424–430.
- EHRENBERG, C. G. 1832. Beiträge zur Kenntnis der Organisation der Infusorien und ihrer geographischen Verbreitung, besonders in Siberien. *Abhandlungen der Preussischen Akademie der Wissenschaften*, **1830**, 1–88.
- 1843. Über die Verbreitung des jetzt wirkenden kleinsten organischen Lebens in Asien, Australien und Afrika und über die vorherrschende Bildung auch des Oolithkalkes der Juraformation aus kleinen polythalamischen Thieren. *Verhandlungen der Preussischen Akademie der Wissenschaften*, **1843**, 100–106.
- 1873. Grössere Felsproben des Polycystinen-Mergels von Barbados mit weiteren Erläuterungen. *Monatsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin*, **1873**, 213–263.
- EVITT, W. R. 1985. *Sporopollenin dinoflagellate cysts: their morphology and interpretation*. American Association of Stratigraphic Palynologists Foundation, Austin, Texas, xv + 333 pp.
- FENSOME, R. A., TAYLOR, F. J. R., NORRIS, G., SARJEANT, W. A. S., WHARTON, D. I. and WILLIAMS, G. L. 1993. A classification of living and fossil dinoflagellates. *Micropaleontology, Special Publication*, **7**, 1–334.
- GOCHT, H. 1983. Morphogenetische Deutung und Bezeichnung ausgewählter Merkmale bei Dinoflagellaten-Zysten. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1983**, 257–276.
- HAECKEL, E. 1894. *Entwurf eines natürlichen Systems der Organismen auf Grund ihrer Stammesgeschichte, Erster Teil: Systematische Phylogenie der Protisten und Pflanzen*. Georg Reimer, Berlin, 400 pp.
- HARDING, I. C. 1988. Thecamorphic features of the early Cretaceous dinocyst *Subtilisphaera terrula*. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1988**(1), 49–63.
- JUKES-BROWNE, A. J. and HARRISON, J. B. 1892. The geology of Barbados, Part 2. The oceanic deposits. *Quarterly Journal of the Geological Society, London*, **48**, 170–226.
- KAMPTNER, E. 1927. Beitrag zur Kenntnis adriatischer Coccolithophoriden. *Archiv für Protistenkunde*, **58**, 173–184.
- LANGHANS, V. H. 1925. Gemischte Populationen von *Ceratium hirundinella* (O.F.M.) Schrank und ihre Deutung. *Archiv für Protistenkunde*, **52**, 585–602.
- LARUE, D. K. and SPEED, R. C. 1984. Structure of the accretionary complex of Barbados, II: Bissex Hill. *Bulletin of the Geological Society of America*, **95**, 1360–1372.
- LEFÈVRE, M. 1933a. Recherches sur les péridiniens fossiles des Barbades. *Bulletin Museum d'Histoire Naturel Paris, serie 2*, **5**, 415–418.
- 1933b. Les Peridinites des Barbades. *Annales de Cryptogamie Exotique*, **6**, 215–229.
- LENTIN, J. K. and WILLIAMS, G. L. 1973. Fossil dinoflagellates: index to genera and species. *Geological Survey of Canada, Paper*, **73-42**, 1–176.
- — 1993. Fossil dinoflagellates: index to genera and species 1993 edition. *American Association of Stratigraphic Palynologists, Contributions Series*, **28**, viii + 856 pp.
- LEAVANDER, K. M. 1894. Materialien zur Kenntnis der Wasserfauna in der Umgebung von Helsingfors, mit besonderer Berücksichtigung der Meeresfauna. I. Protozoa. *Acta Societatis pro Fama et Flora Fennica*, **12**, 1–115.

- LEWIS, J. 1990. The cyst-theca relationship of *Oblea rotunda* (Diplopsalidaceae, Dinophyceae). *British Phycological Journal*, **25**, 339–351.
- and BURTON, P. 1988. A study of newly excysted cells of *Gonyaulax polyedra* (Dinophyceae) by electron microscopy. *British Phycological Journal*, **23**, 49–60.
- MCCLEAN, D. M. 1973. A problematical dinoflagellate from the Tertiary of Virginia and Maryland. *Palaeeontology*, **16**, 729–732.
- MASURE, E. 1990. L'origine et la phylogénie des Peridiniaceae (Dinoflagellés) d'après les témoins fossiles. *Revue de Micropaléontologie*, **33**, 219–232.
- MULLER, O. F. 1773. *Vermium terrestrium et fluvialium*. Hainek et Faber typis Martini Halleger, Havniae et Lipsiae, **1**, xxxii + 135 pp.
- NORRIS, G. and SARJEANT, W. A. S. 1965. A descriptive index of genera of fossil Dinophyceae and Acritarcha. *Paleontological Bulletin of the New Zealand Geological Survey*, **40**, 1–72.
- PASCHER, A. 1914. Über Flagellaten und Algen. *Bericht der Deutschen Botanischen Gesellschaft*, **36**, 136–160.
- RIEDEL, W. R. and SANFILIPPO, A. 1970. Radiolaria, Leg 4, Deep Sea Drilling Project. *Initial Reports of the Deep Sea Drilling Project*, **4**, 503–575.
- SANFILIPPO, A., WESTBERG-SMITH, M. J. and RIEDEL, W. R. 1985. Cenozoic radiolaria. 631–712. In BOLLI, H. M., SAUNDERS, J. B. and PERCH-NIELSEN, K. (eds). *Plankton stratigraphy*. Cambridge University Press, Cambridge, viii + 1032 pp.
- SPEED, R. C. 1983. Structure of the accretionary complex of Barbados, I: Chalky Mount. *Bulletin of the Geological Society of America*, **94**, 92–116.
- 1985. New views on the geology of Barbados. *Transactions of the 4th Latin American Geological Congress (Port of Spain, Trinidad, 1979)*, **2**, 929–942.
- and LARUE, D. K. 1982. Barbados: architecture and implications for accretion. *Journal of Geophysical Research*, **87** (B5), 3633–3643.
- TANGEN, K., BRAND, L. E., BLACKWELDER, P. L. and GUILLARD, R. R. L. 1982. *Thoracosphaera heimii* (Lohmann) Kamptner is a dinophyte: observations on its morphology and life cycle. *Marine Micropaleontology*, **7**, 193–212.
- TORIUMI, S. and DODGE, J. D. 1993. Thecal apex structure in the Peridiniaceae (Dinophyceae). *European Journal of Phycology*, **28**, 39–45.
- VOZZHENNIKOVA, T. F. 1963. Klass Peridineae (Dinoflagellateae). Peridinei, ili dinoflagellaty. 171–186. In KISELEVA, A., VACHRAMEEVA, V. A., RADCHENKO, G. P. and TACHMADZHANA, A. L. (eds). *Tip Pyrrophyta. Pirofitovye Vodorosli*. In ORLOV, Y. A. (ed.). *Osnovy Palaeeontologii: Vodorosli, Mochoobraznie, Psilofitovye, Planovidnie, Chlenistostebelnie, Paprotniki*, **14**. Nedra Press, Moscow. [In Russian].
- 1967. *Iskopaemye peridinei Yurskikh, Melovykh i paleogenovykh otlozhenii SSSR*. Izdatel Nauka, Moscow, 347 pp. [In Russian].
- WALL, D. and DALE, B. 1971. A reconsideration of living and fossil *Pyrophacus* Stein, 1883 (Dinophyceae). *Journal of Phycology*, **7**, 221–235.

IAN C. HARDING

Department of Geology  
University of Southampton  
Highfield  
Southampton, SO17 1BJ, UK

JANE LEWIS

Applied Ecology Research Group  
School of Biological and Health Sciences  
University of Westminster  
115, New Cavendish Street  
London W1M 8JS, UK

Typescript received 21 October 1993

Revised typescript received 2 February 1994